

## Seasonal changes in the frequency of intrusion by web spiders into webs abandoned by *Metleucauge kompirensis* (Araneae: Tetragnathidae)

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**Abstract** — To reveal the factors that influence web-intrusion frequency by other web-building spiders, I investigated seasonal changes in the frequency of intrusion by spiders into webs abandoned by *Metleucauge kompirensis* (Tetragnathidae). I analyzed the effects of various conditions, including the size and density of host webs, and the life histories of intruding species. Intruders were mainly *Tetragnatha praedonia* of various size-classes, as well as small individuals of *M. kompirensis*. The average number of intruders per web was low between April and June because of the low density of intruding species and the high density of host webs. Thus, competition among intruders was probably not intense during this time. Early in the season, most insects remained in host webs were not consumed by intruders during the daytime, but may have been consumed with web silks by the web owners in the evening, before they constructed new webs. On the other hand, the average number of intruders per web was very large between July and early September. This may have been due to the low density of host webs and the emergence of newly born *M. kompirensis* spiderlings. The average number of insects remaining in webs during the daytime was low, as most insects were removed by intruders in the morning, when there was strong competition among intruders. Thus, the frequency of intrusion seems to depend primarily on the density of host webs and the density of intruding species.

**Key words** — frequency of intrusion, seasonal change, density of host webs, density of intruders, size of host webs

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### Introduction

Although web spiders usually capture prey in their own webs, they sometimes intrude into the webs of other spiders and steal prey insects (Binford & Rypstra 1992; Buskirk 1975a, b; Lahmann & Eberhard 1979; Lubin 1974; Nyffeler & Benz 1980; Rypstra 1979; Rypstra & Binford 1995; Yoshida 1977a, b, 1986, 1988, 2001). Intrusion into neighboring webs is often observed in communal or colonial species (Binford & Rypstra 1992; Buskirk 1975a, b; Eberhard 1978; Fowler & Diehl 1978; Lahmann & Eberhard 1979; Lubin 1974; Rypstra 1979). Such intrusion also occurs in solitary species at high densities (Nyffeler & Benz 1980; Yoshida 1977a, 2001).

I previously reported that two tetragnathid spiders (various size-classes of *Tetragnatha praedonia* and spiderlings of *Metleucauge kompirensis*) frequently intrude into webs abandoned by adult *M. kompirensis* females in July and August, and consume many insects

remained in the webs (Yoshida 2001). However, the frequency of intrusion (the average number of intruders per host web) is very low in spring, as is shown in this study. This difference in intrusion frequency between the two seasons may be attributable to the differences of the environmental conditions. The intrusion frequency may be high when: 1) the density of host webs are low because many intruders concentrate in less number of host webs; 2) the host webs are large (Yoshida 2001) because there is large space for intruders; 3) there are many insects remained in host webs because intruders can get more insects; and 4) the density of intruding species is high because there are many spiders near host webs. These factors change as the season progresses. For example, the host spider *Metleucauge kompirensis* matures in June and July (Yoshida 1977a, unpublished data), so the web may be largest in the season, and the density of the host may decrease rapidly afterwards. Condition of a factor may change with that of another factor. For example, the density of host webs may

negatively correlate with the web size, because host webs become larger as the hosts grow, whereas web density decreases due to the death of some hosts. The number of insects per host web may positively correlate with the web size. On the contrary, the density of intruding species may not be related to other factors.

So, I report here the seasonal changes in the frequency of intrusion into abandoned webs of *M. kompirensis*, and analyze the effects of various factors, including the density of host webs, the web size, and the density of intruding species, on the frequency of intrusion of three web spiders.

## Materials and Methods

### Spiders

*Metleucauge kompirensis* and *Tetragnatha praedonia* (Tetragnathidae) construct horizontal orb webs above streams. *Leucauge magnifica* makes such webs both at banks and above streams. *M. kompirensis* hunts for prey on the web at night, though the small individuals hunt also in the daytime. On the other hand, *L. magnifica* hunts all day. *T. praedonia* hunts mainly at night, though it sometimes hunts in the daytime. Most individuals of *M. kompirensis* leave their webs in the morning to rest under leaves or twigs. The spiders usually destroy their webs before leaving, but some webs are left intact during the day (Yoshida 1977a, 2001, unpublished data).

### Field investigation

I conducted this investigation from April to October 1980 at the Hinokidani River, a 1- to 2-m-wide branch of the Kamo River in Kyoto, Japan. The stream was shaded in various places by vegetation growing along the banks. I investigated between the hours of 10:00 and 16:30. I counted the number of insects and intruders in abandoned webs of *M. kompirensis* found above the stream. I then collected about one-third of the intruders found in the field, identified them, and measured their body lengths in the laboratory. I also measured the major (R) and minor (r) axes of abandoned webs, from which I calculated the web area using the formula:  $S = \pi Rr/4$ . In order to measure the density of abandoned webs, I counted the number of abandoned webs in an area 2.5 m  $\times$  7.0 m. In order to estimate the densities of intruding species, I collected spiders by sweeping shrubs and herbaceous vegetation along the stream banks.

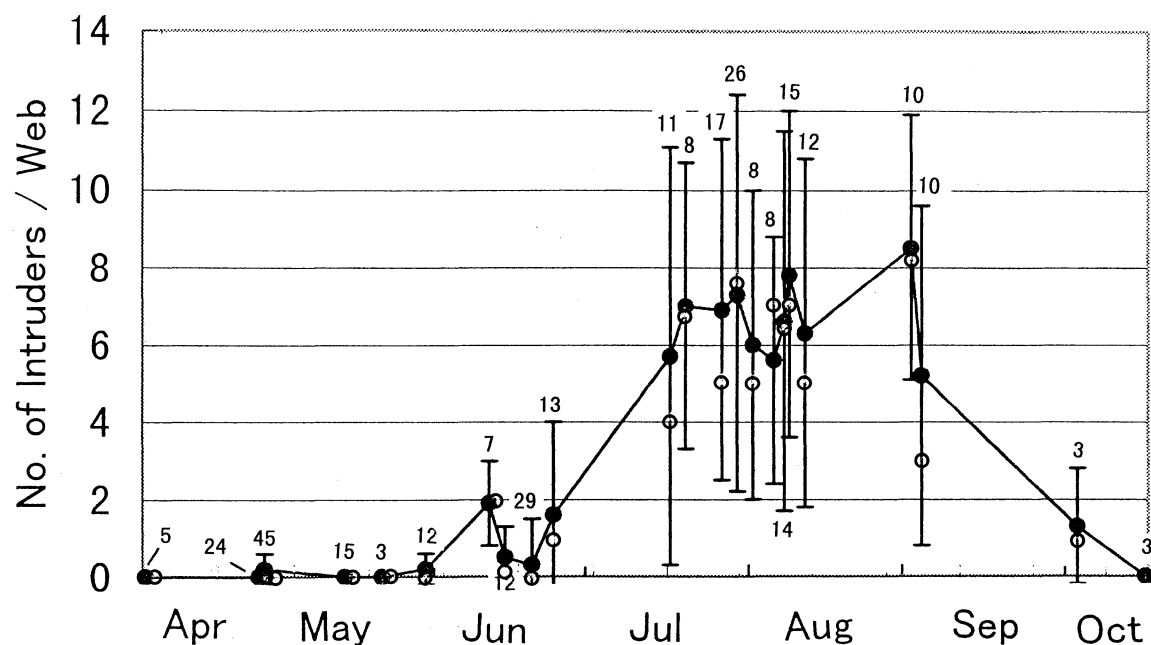
## Results

Three web-building species *Metleucauge kompirensis*, *Tetragnatha praedonia* and *Leucauge magnifica* were recorded as intruders into abandoned webs of *M. kompirensis*. The average number of intruders per web was near zero in April and May, and then increased slightly (to  $<2$ ) in June. It increased rapidly in July and remained  $>5$  until early September. In the season, the standard deviations were very large, and the medians were smaller than the averages in most cases. It may mean that some webs with many intruders raised the averages. The average number decreased to  $<2$  in October (Fig. 1).

Table 1 shows the composition of species invading abandoned webs. In total, *M. kompirensis* made up 73.1% of intruding species and *Tetragnatha praedonia* made up 23.6%, and the percentage of *Leucauge magnifica* was low. The percentages of these three species differed among months. While the percentage of *M. kompirensis* was very low from April to June, it increased through July and was very high in August and September. In contrast, the percentage of *T. praedonia* was high from April to July, but decreased in August. *L. magnifica* intruded with relatively high frequency between April and June, however, it decreased after July. Intruding *M. kompirensis* and *L. magnifica* were mainly small individuals  $<4$  mm long, whereas various size-classes of *T. praedonia* intruded (Fig. 2).

The density of abandoned webs was low in early April, probably because many spiders did not construct webs as a result of low ambient temperatures. Web density was highest in late April, and then decreased until August, after which it was very low (Fig. 3A). The average web area measured around 1000 cm<sup>2</sup> until mid-May, and then increased rapidly. The average web area increased to  $>4000$  cm<sup>2</sup> between mid-July and early August. In the season, the standard deviations were large, and the medians were smaller than the averages (Fig. 3B).

The density of intruding species was low from April through June, increased rapidly, and then peaked in late August. The density of *M. kompirensis* increased rapidly in early August, due to the emergence of spiderlings. Similarly, many *L. magnifica* spiderlings emerged in late August (Fig. 4). Many prey insects were left in abandoned webs between late April and late June, but only a few insects were found in early April, July, and August (Fig. 5).



**Fig. 1.** Seasonal changes in the number of intruders per web. Solid and open circles represent the averages and the medians, respectively. Bars and numerals on top of the bars represent standard deviations, and the numbers of webs investigated, respectively.

**Table 1.** Seasonal change of number and relative frequency (in parentheses) of three intruding species, *Metleucauge kompirensis*, *Tetragnatha praedonia*, and *Leucauge magnifica*.

Month	Number of intruders			Total
	<i>M. kompirensis</i>	<i>T. praedonia</i>	<i>L. magnifica</i>	
April to June	1( 2.2)	31(67.4)	14(30.4)	46
July	87(55.4)	70(44.6)	0( 0.0)	157
August	324(86.2)	46(12.2)	6( 1.6)	376
September	50(94.3)	2( 3.8)	1( 1.9)	53
Total	462(73.1)	149(23.6)	21( 3.3)	632

## Discussion

The frequency of intrusion (the number of intruders in a host web) may be influenced by some ecological factors (Table 2). High host density, small host webs, less number of insects left in host webs, and low intruder's density may lead to the low frequency of intrusion. From April to June, the density of host webs was high, the size of host webs was small, many insects were left there, and the density of intruding species was low. In the season, the frequency of intrusion was low (Table 3). This result is consistent with the forecast A (Table 2), except for many insects left there. It may mean that the low frequency of intrusion is due to the high host density, the small web size, and the low density of intruding species. It may represent also that the

number of insects in host webs does not affect to the frequency of intrusion so much in this case. Most insects might be consumed by web owners with the web silks in the evening, before new webs are constructed.

On the other hand, in July and August, the frequency of intrusion was very high, and most of intruders were *M. kompirensis*. In July, many *M. kompirensis* spiderlings emerged, and in August, the density of host webs decreased rapidly. In the season, the size of host webs was large. This result is consistent with the forecast B (Table 2), except for the small number of insects left there. It may mean that the high frequency of intrusion is due to the high density of intruding species, the low host density, and the large web size. The small number of insects found in this study does not mean that few insects were left in host webs at the beginning of the day, but rather, that most insects had been removed

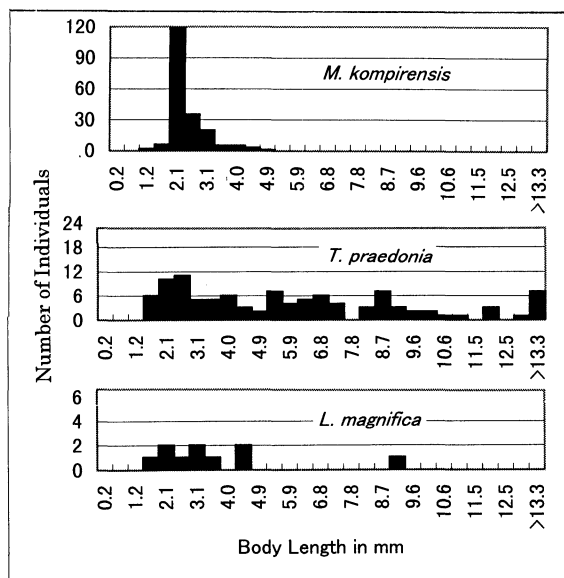


Fig. 2. Frequency distribution of body length of intruders.

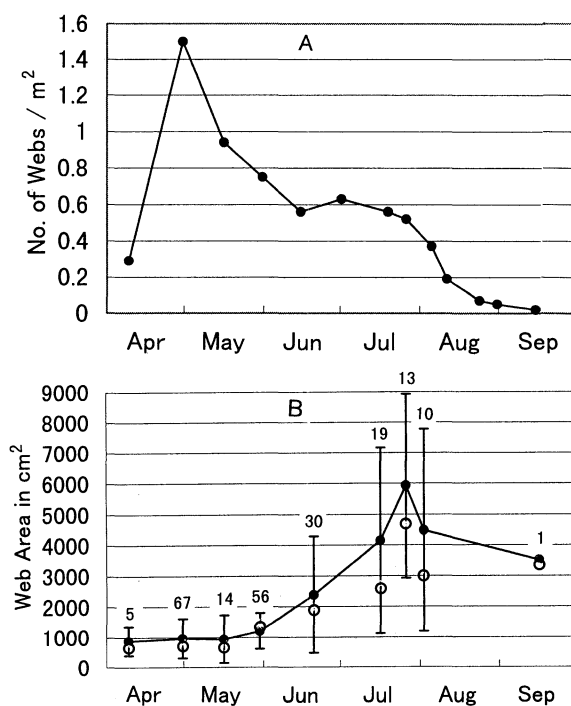


Fig. 3. A. Seasonal changes in the density of abandoned webs. B. Seasonal changes in the area of webs abandoned by *M. kompirensis*. For other explanations see Fig. 1.

during the morning. Most host webs had many insects in early morning (Yoshida 2001).

The low frequency of intrusion by *L. magnifica*

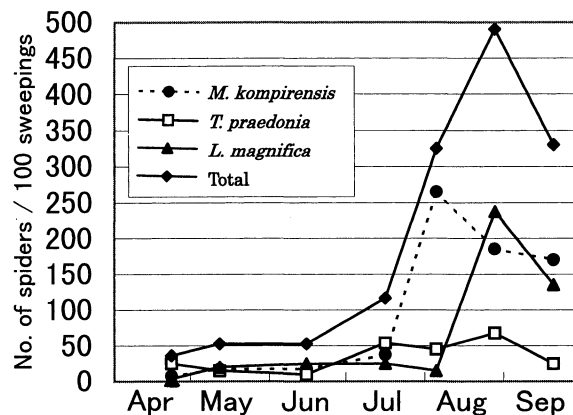


Fig. 4. Seasonal changes in the density of spiders collected by sweeping on the stream banks.

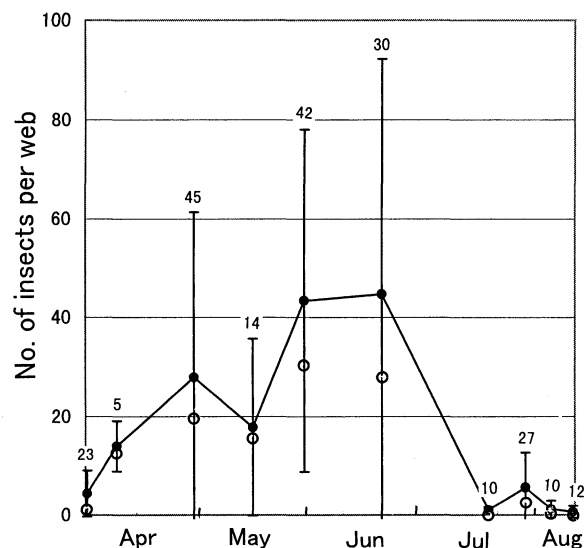


Fig. 5. Seasonal changes in the number of insects left in abandoned webs. Explanations as in Fig. 1.

Table 2. Expected relationships between the frequency of intrusion (the average number of intruders per host web) and some ecological factors.

	Forecast A	Forecast B
Frequency of intrusion	low	high
Host density	high	low
Host-web size	small	large
Number of insects per web	small	large
Density of intruding species	low	high

despite of its high density during the season suggests that this species is less kleptoparasitic than *M. kompirensis* and *T. praedonia*. This may be due to the low density of *L. magnifica* spiderlings above stream though it was very high at banks. They usually made

**Table 3.** Observed seasonal change in relationships between the frequency of intrusion and some ecological factors.

Season	April-June	July-August
Frequency of intrusion	low	high
Host density	high	low
Host-web size	small	large
Number of insects per web	large	small
Density of intruding species	low	very high

their webs at banks. Few webs were found in the central open space above the stream where *M. kompirensis* made their webs (Yoshida 1974). *L. magnifica* spiderlings often invaded the webs of adult *L. magnifica* whose owners were removed artificially (Yoshida, unpublished data), so they also seem to be somewhat kleptoparasitic. Adult *L. magnifica* females sometimes intrude into the webs of *L. magnifica*, *M. kompirensis* and *T. praedonia* (Yoshida 1975a, b). *L. magnifica* also intrudes into the webs of *Nephila clavata* (Yoshida 1986, 1988).

Why is it only small *M. kompirensis* individuals that intrude into other webs? It may be due to a difference in the diurnal rhythms of large and small *M. kompirensis* individuals. Most adult *M. kompirensis* females emerge from their retreats in the evening and hunt on their webs at night (Yoshida 1977a), whereas the spiderlings are active in the daytime (Yoshida 2001; and this study) as well as at night (Yoshida, unpublished data). Fowler & Diehl (1978) also reported a difference in the diurnal rhythms of juveniles and adults in a colonial orb-weaving spider, *Eriophora bistrata* (Araneidae). But, why are the *M. kompirensis* spiderlings active in the daytime? It may be a behavioral adaptation that allows them to intrude into the abandoned adult webs. Although *M. kompirensis* spiderlings do construct tiny webs, not one of 34 webs examined in the day time contained prey insects in August 1984 (Yoshida, personal observation). Therefore, stealing prey in the daytime may be a better tactic for the spiderlings than web-making. On the other hand, *T. praedonia* individuals of various sizes intrude into other spiders' webs, which suggests that both juvenile and adult *T. praedonia* show kleptoparasitic behavior.

In order to capture prey insects, web spiders may consider cost-performance when choosing between making their own webs or intruding into other webs, if there are neighboring webs available. Intrusion may be a better tactic than web-making when host webs are abundant. Because they are undefended, the abandoned webs

of *M. kompirensis* may be more attractive to intruders than occupied webs (Yoshida 2001, this study). On the other hand, web-making may be a better tactic than intrusion when host webs are scarce. Cangioli (1997) showed an example: the kleptoparasitic spider, *Argyrodus trigonum* (Theridiidae), both intrudes into host webs and captures prey insects in its own webs. *A. trigonum* construct more of their own webs when there are less host webs, which suggests that when web density is low, prey capture is more effective using their own webs than using host webs.

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タニマノドヨウグモの放置網に侵入する造網性クモ類の侵入頻度の季節的变化 (pp. 117-122)

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クモ網への造網性クモ類の侵入に関与する諸要因を明らかにするために、タニマノドヨウグモが放置した網へ侵入する造網性クモ類の頻度の季節的变化を調べた。関与する要因として、ホスト網のサイズと密度、侵入種の生活史と密度が調べられた。侵入者はおもに、タニマノドヨウグモの仔グモとさまざまなサイズのアシナガグモであった。網あたりの侵入者数の平均は、侵入種の密度が低くホスト網の密度が高いために、4月から6月までは低かった。これに対して7月から9月上旬にかけては、侵入者は非常に多かった。これは、ホスト網の密度が低いことと、7月に生まれたタニマノドヨウグモの仔グモの出現によると思われる。このように、侵入頻度は一義的には、ホスト網の密度と侵入種の密度に依存していると思われる。

中国のアシダカグモ科 1. 新シノニムと転属, タイプ指定つき, 既知種のリスト (pp. 123-134)

Peter Jäger<sup>1</sup>, Chang-Min Yin<sup>2</sup> (<sup>1</sup>Institut für Zoologie, Johannes Gutenberg-Universität, Germany; <sup>2</sup>Hunan Normal University, P. R. China)

中国のアシダカグモ科の最初の分類学的改訂として、これまでに中国から記録されている3亜科8属51種のリストを掲げた。個々の種の詳細なタイプ標本のデータ、既知分布を示した。次の種について転属をおこなった: *Olios menghaiensis* (Wang 1990), *Olios tiantongensis* (Zhang & Kim 1996), *Pseudopoda bibulba* (Xu & Yin 2000) *Sinopoda dayong* (Bao, Yin & Yan 2000 (以上旧 *Heteropoda*)), *Olios nanningensis* (Hu & Ru 1988) (旧 *Micrommata*), *Pseudopoda marsupia* (Wang 1991) (旧 *Sinopoda*)。次の種は新規にシノニムと認められた: *Heteropoda guangdongensis* Yin, Yan & Kim 2000 は *Olios nanningensis* (Hu & Ru 1988) の, *Micrommata hainanensis* He & Hu 2000 は *Olios nanningensis* (Hu & Ru 1988) の, *Heteropoda shimen* Yin, Peng, Yan & Bao 2000 は *Heteropoda venatoria* (Linnaeus 1767) の, *Thelcticopis jiulongensis* Zhang & Kim 1996 は *Thelcticopis severa* (L. Koch 1875) のそれぞれジュニ

アシノニム。次の種のシノタイプ, レクトタイプ, パラレクトタイプを指定した: *Pseudopoda exiguides* (Song & Zhu 1999), *Sinopoda pengi* Song & Zhu 1999, *Sinopoda wangi* Song & Zhu 1999. また *Heteropoda zhangii* Song & Zhu 1999 は無効学名である。(和訳: 編集委員会)

旧北区東部からのメキリグモ属 (ワシグモ科) の1新種と他の数種の新記録 (pp. 135-144)

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ワシグモ科メキリグモ属 *Gnaphosa* の *borea* 種群に属する1新種 *G. banini* をモンゴルから記載するとともに、本種群 (*G. borea* Kulczyński 1908, *G. chola* Ovtsharenko & Marusik 1988, *G. microps* Holm 1939, *G. oritis* Chamberlin 1922, *G. banini*) の雄の識別形質を示した。 *G. ilika* Ovtsharenko et al. 1922, *G. pseudoleporiona* Ovtsharenko et al. 1992 の雄を図示した。また、旧北区東部からの他の *Gnaphosa* 属9種の生物地理学的に興味のもたれる記録を掲げた。(和訳: 編集委員会)

全北区系のクモの1属 *Procerocymbium* Eskov 1989 (サラグモ科) の改訂 (pp. 145-156)

Yuri M. Marusik<sup>1</sup> & Seppo Koponen<sup>2</sup> (<sup>1</sup>IBPN RAS, Russia; <sup>2</sup>Zoological Museum, University of Turku, Finland)

サラグモ科 *Procerocymbium* Eskov 1989 とその基準種 *P. sibiricum* Eskov 1989 を再記載し、3新種 *P. jenseicum* (中部シベリア), *P. buryaticum* (トランスバイカルと南ヤクーチア), *P. dondalei* (ユーコン地方) を記載した。本属の他の属との関係についても論議した。(和訳: 編集委員会)

日本産ヒメグモ亜科 (クモ目: ヒメグモ科) の属および種の検討 (pp. 157-181)

吉田 哉 (〒990-2484 山形市竈田2丁目7番16号)

日本産のヒメグモ亜科 Theridiinae Sundevall 1833 の属および種の検討をおこなった。ヒメグモ亜科は雄触肢の杯葉内側に頭巾状の小杯葉があることが特徴で、ほとんどの属に間疣がない。Monetinae Simon 1894 お